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Motile curved bacteria are Pareto-optimal

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Curved rods are a ubiquitous bacterial phenotype, but the fundamental question of why they are shaped this way remains unanswered. Through in silico experiments, we assessed freely swimming straight- and curved-rod bacteria of a wide diversity of equal-volume shapes parameterized by elongation and curvature, and predicted their performances in tasks likely to strongly influence overall fitness. Performance trade-offs between these tasks lead to a variety of shapes that are Pareto-optimal, including coccoids, all straight rods, and a range of curvatures. Comparison with an extensive morphological survey of motile curved-rod bacteria indicates that the vast majority of species fall within the Pareto-optimal region of morphospace. This result is consistent with evolutionary trade-offs between just three tasks: efficient swimming, chemotaxis, and low cell construction cost. We thus reveal the underlying selective pressures driving morphological diversity in a widespread component of microbial ecosystems.

motility | shape | morphology | swimming | evolution

In stark contrast to the macroscopic realm of multicellular plants and animals, in the microscopic world it remains a challenge to attribute function to any of the considerable morphological diversity that exists (1, 2). Even superficially simple traits such as the curvature of many rod-shaped bacteria have eluded evolutionary explanations, despite the ubiquity of such morphological variations. For example, while coccoids and “rods” comprise the vast majority of bacteria in the ocean, curved rods account for up to a quarter of these (3), sometimes outnumbering straight rods (4). Also observed but rarely quantified in most other habitats (5–8), curved bacteria have invested heavily in complex genetic machinery to generate and maintain their shapes (9), but we have almost no understanding of the benefits their curvature confers (1). While the biochemical and genetic mechanisms of cell growth and the maintenance of shape have received considerable attention (10–13), the costs or benefits of a particular shape have received almost none (but see refs. 14 and 15). Understanding the links between form and function is a cornerstone of modern biology, yet no studies have addressed why curvature has evolved in many bacterial clades (5–8).

The microscale physics relevant to bacteria makes addressing the physical consequences of their shapes particularly nonintuitive (16). One hypothesis is that, at microscopic scales, shape generally has no bearing on fitness (17). However, while there appears to be limited support for this “neutral morphology” theory (18), several lines of empirical evidence suggest that, just as for larger organisms, selective pressures influence microbial cell shape. Bacterial cell shape is (i) heritable, with some morphologies evolving independently many times; (ii) has high diversity, yet is typically uniform (excluding pleomorphism) within species; and (iii) is known to be actively modified in response to environmental changes (1).

Free-swimming cells are ubiquitous, comprise a large fraction (up to 70%) of the bacteria in the oligotrophic marine environment (19), and are part of the life cycle of many biofilm-forming species. However, the streamlining principles that explain the shapes of many swimming animals work very differently at the microscale (20). The most efficient shape for an ellipsoidal swimmer at this scale is similar to a rugby ball, but most rod-shaped bacteria are more elongated than this optimum (16). Dusenbery (16) suggests that motile bacteria are under selective pressure to elongate

without bound to improve chemotactic ability, since such cells are much more resistant to random course changes imposed by Brownian motion. Hence, the diversity of elongated shapes in bacteria may well be due to evolutionary trade-offs between a number of tasks (21), such as chemotaxis and swimming efficiency. Might bacterial curvature have evolved due to similar trade-offs?

Here, we address a broad bacterial morphospace of all free-swimming curved rods, straight rods, and spheres. First, we survey the literature in search of microscopy data on curved bacteria, inserting them into a 2D parameter space of elongation and curvature to quantify their morphological diversity. In a major effort involving tens of thousands of numerical simulations, we then quantify performance throughout this morphospace in several physiologically relevant tasks likely to contribute to overall evolutionary fitness, revealing the selective advantages (and disadvantages) of curvature and elongation. Finally, from these disparate performance landscapes, we use the concept of Pareto optimality (21) to analyze the diversity of observed rod morphologies through the lens of evolutionary trade-offs between tasks. [We use the term “performance landscape” in favor of the well-known “fitness landscape” concept (22) to distinguish performance in individual tasks from overall evolutionary fitness.] While previous work (21) has approached this type of problem by leveraging abundant data on the ecology of macroscopic organisms (e.g., birds, bats, ants), such data are sparse or nonexistent at the scales relevant to bacteria. Despite this major obstacle, our direct computations of Pareto optimality allow us to identify which tasks likely constrain the evolution of shape within this morphologically diverse polyphyletic group. We thus

Significance

Bacteria exhibit a bewildering diversity of morphologies, but despite their impact on nearly all aspects of life, they are frequently classified into a few general categories, usually just “spheres” and “rods.” Curved-rod bacteria are one simple variation observed in many environments, particularly the ocean. However, why so many species have evolved this shape is unknown. We show that curvature can increase swimming efficiency, revealing a widely applicable selective advantage. Furthermore, we show that the distribution of cell lengths and curvatures observed across bacteria in nature is predicted by evolutionary trade-offs between three tasks influenced by shape: efficient swimming, the ability to detect chemical gradients, and reduced cost of cell construction. We therefore reveal shape as an important component of microbial fitness.

Author contributions: R.S., D.J.S., and S.H. designed research; R.S. and T.H. performed research; R.S. and D.J.S. contributed new reagents/analytic tools; R.S. and T.H. analyzed data; and R.S. and S.H. wrote the paper.

The authors declare no conflict of interest.

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link form and function at the microscale and pave the way toward a broader understanding of bacterial diversity.

Survey of Curved Bacteria Shapes

We surveyed the literature for micrographs of motile, flagellated curved-rod bacteria (*Methods*, *Survey of Observed Shapes*, and *SI Appendix*, section 1). Since a wide range of motile straight rods (from coccoids to filaments) has previously been reported (16), we included these in our subsequent calculations but focused our efforts on surveying visibly curved cells. Individual cells were segmented using MicrobeJ (23) (*Methods*, *Survey of Observed Shapes*, and *SI Appendix*, Fig. S1 and section 1) and fitted to a simple geometric model parameterized by elongation (\mathcal{L}) and centerline “curvature” (\mathcal{K}), both dimensionless and thus independent of length scale (Fig. 1, *Inset*; *Methods*, *Model Geometry*; *SI Appendix*, section 6.1). (For brevity and accessibility, instead of the typical mathematical meaning, we use the term “curvature” loosely to describe the dimensionless fraction of a full circumference formed by the cell centerline.) The survey (Fig. 1 and *Dataset S3*) highlights the diversity of shapes within our curved-rod parameter space: Short bean-, comma-, and long hotdog-like shapes can all be found in nature, with a few exceptionally elongated species beyond $\mathcal{L} = 10$ (*SI Appendix*, Fig. S2). Of the 11 phyla, 98 genera, and 205 species, notable members of the dataset include *Bdellovibrio* spp. (which feeds on other bacteria, including human and animal pathogens), and *Vibrio cholerae* and *V. vulnificus*, both capable of causing serious illness in humans. The median curved rod ($\mathcal{L} = 3.7$, $\mathcal{K} = 0.14$) corresponds to a rod with limited curvature (similar to *Vibrio ruber*), and 50% of all curved species fall within $\mathcal{L} = 2.3$ –4.9 and $\mathcal{K} = 0.05$ –0.25. There is a factor of 10 variation in diameter of an equal-volume sphere [i.e., equivalent spherical diameter (ESD)], but with no discernible correlation between size (for our purposes, ESD) and shape (\mathcal{L} vs. ESD, $n = 220$, $r^2 = 0.001$, $P = 0.582$; \mathcal{K} vs. ESD, $n = 220$, $r^2 = 0.005$, $P = 0.298$), we do not consider size further (*SI Appendix*, section 2). There is, however, a weak decreasing trend in curvature versus elongation (\mathcal{L} vs. \mathcal{K} , $n = 223$,

$r^2 = 0.028$, $P = 0.012$). Although toroidal bacterial morphologies do exist (*SI Appendix*, section 1), there is a conspicuous lack of motile species that are more than semicircular (Fig. 1).

Swimming Efficiency

Given that curved bacteria fill a particular region of the theoretical morphospace (Fig. 1), it is natural to ask why bacteria might be curved at all, why some are as curved as they are, and why not all conceivable curved-rod morphologies are found in nature. We first hypothesized that cell curvature might enhance the swimming speed of a bacterium, given a certain power expenditure. That is, curvature might increase Swimming Efficiency, defined as the ratio of power required to translate an equal-volume sphere to the mechanical power dissipated by the flagellar motor: $\Psi_{\text{swim}} = 6\pi\bar{a}\mu\bar{U}_{\text{swim}}^2/\bar{P}^M$, where \bar{a} is equivalent cell radius (0.62 μm for all cells here), μ is dynamic viscosity of water (10^{-9} kg·s $^{-1}$ · μm^{-1}), \bar{U}_{swim} is effective swimming speed, and \bar{P}^M is average power dissipated by the motor (ref. 24; *SI Appendix*, section 10.3). This hypothesis is in line with the results of Phan-Thien et al. (25), who showed that a slightly flattened triaxial ellipsoid is marginally more efficient than the best rotationally symmetric spheroid, as well as Liu et al. (26), who approximated *Caulobacter crescentus* as a straight rod with a tilted off-axis flagellum and found increased efficiency compared with the aligned case. The reason for this is a peculiarity of propulsion by a rotating flagellum—there is a trade-off between minimizing the translational resistance of the body and maximizing its rotational resistance, to reduce the power typically wasted by body counterrotation. Applied to curved rods, this idea suggests that an optimal curvature should exist, since curvature should increase both translational and rotational resistance.

Using a regularized Stokeslet Boundary Element Method (*Methods*, *Numerical Solution for Swimming Kinematics and Rotational Diffusion*, and *SI Appendix*, sections 3–9), we simulated the detailed kinematics of freely swimming curved rods propelled by rotating flagella (Fig. 2B and *SI Appendix*, Fig. S3 and *Movie S1*) over a broad theoretical morphospace spanning nearly all our observed body shapes as well as spheres, straight rods, and rings (Fig. 2A and *SI Appendix*, Fig. S14). All shapes were constrained to be equal volume ($1\ \mu\text{m}^3$, similar to *E. coli*) to focus on variation in shape, not size, although we note that our definition of Ψ_{swim} is scale-invariant regardless. While our focus was bacterial body shape, flagellum shape also affects swimming performance. Since there is a profound scarcity of detailed data on flagellar morphology, we chose to pair each body shape with its optimal helical flagellum (i.e., optimal amplitude, wavelength, and number of wavelengths: Fig. 2D and *SI Appendix*, Fig. S16 and section 11.1) that maximizes Ψ_{swim} to reduce artificial biases in our results, despite this task requiring >100,000 CPU hours. We thus generated a performance landscape for Swimming Efficiency over diverse curved bacterial shapes (Fig. 3A).

Surprisingly, we found that over the entire morphospace, the globally optimal Swimming Efficiency is achieved not by a curved rod but a straight, slightly elongated rod comparable to a medicine capsule ($\mathcal{L} = 1.46$, $\mathcal{K} = 0$; Fig. 3A). However, this shape has a Swimming Efficiency advantage of just 2% over a spherical body, in general agreement with previous studies of ellipsoidal cells (16, 24, 25) (*SI Appendix*, Fig. S19), and is only 0.3% better than the semicircular curved rod located at a local maximum in the performance landscape ($\mathcal{L} = 4.0$, $\mathcal{K} = 0.70$). In fact, a diverse range of shapes exhibit essentially the same efficiency, with only long straight rods having substantially reduced performance compared with a sphere (*Movie S1*).

Intriguingly, the optimal curvature \mathcal{K} for a given elongation \mathcal{L} is approximately constant (~ 0.65) beyond $\mathcal{L} = 4$, with efficiencies within a few percent of that of a sphere up to $\mathcal{L} = 10$. However, even modest curvature (e.g., $\mathcal{K} = 0.2$) allows a highly elongated

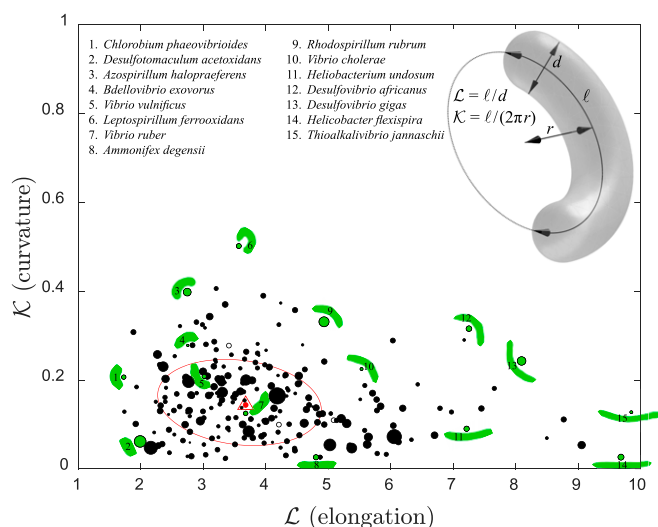


Fig. 1. Survey of extant curved-rod morphologies, with geometric parameters and definitions of dimensionless shape parameters \mathcal{L} and \mathcal{K} (*Inset*). The circles represent species median shapes based on segmented images, with circle radius proportional to equivalent spherical diameter (ESD) when scale data available (filled) or overall median ESD when not (open). The smallest ellipse containing 50% of all species is shown in red, and overall median species shape (and ESD) is depicted by a red filled circle, highlighted by a triangle. Silhouetted individuals (green), rescaled to constant volume, are shown for selected species (green filled circles).

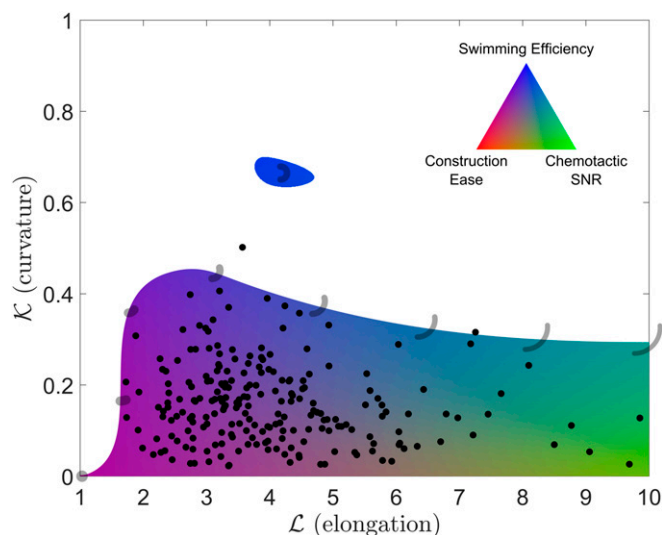


Fig. 5. Pareto-optimal curved-rod morphologies. Colored regions represent the set of shapes that are Pareto-optimal resulting from trade-offs between Swimming Efficiency, Chemotactic SNR, and Construction Ease; white region represents suboptimal shapes; and dots represent observed species medians. Selected simulated morphologies are plotted along the main optimal/sub-optimal Pareto front as well as at the centroid of the disconnected Pareto-optimal “island.” RGB color values were assigned by normalizing performances in each task within the optimal region between 0 and 1. Color thus signifies relative, not absolute, trade-offs between tasks as indicated by the color triangle (*Inset*). Not all colors in the triangle are realized because not all possible trade-offs are realized (e.g., the shapes that excel at Construction Ease also excel at Swimming Efficiency).

contours (Fig. 3 *A* and *C*), local maxima (Fig. 3*A*), nonfinite optimal shapes (Fig. 3*B*), which combine to yield a Pareto-optimal region that is not a simple triangle (Fig. 5) as would be expected under simplifying assumptions (21) (*SI Appendix, section 12*). By considering many combinations of the putative tasks in our analysis of Pareto optimality (*SI Appendix, section 12*), we gain confidence (*SI Appendix, section 13*) in our conclusion that the tasks constraining evolution of curved morphologies are Swimming Efficiency, Chemotactic SNR, and Construction Ease. While we cannot rule out the importance of additional tasks such as navigation through viscoelastic gels (15), avoidance of predation (39), attachment or detachment from surfaces (14, 40), and activities related to life in biofilms (41), our proposed set of three tasks is minimally complex in the sense that this is the minimum number required to explain the diversity of observed morphologies (*SI Appendix, section 12*).

The inclusion of Swimming Efficiency in the small set of critically important tasks shaping the evolution of curved bacteria might seem surprising given the ranges of variation seen in the performance landscapes: Construction Ease and Chemotactic SNR display relatively strong effects of shape, with factors of 3 and 2.2 variation, respectively, over the Pareto-optimal region of morphospace (Fig. 3 *B* and *C*). Although Swimming Efficiency exhibits a factor of 1.5 variation overall, there is far less variability (i.e., 10%) over the majority of considered shapes, particularly those that determine the upper front of the main Pareto-optimal region (Figs. 3*A* and 5). This observation highlights a core difficulty with the evolutionary multiobjective optimization problem—the relative contributions of each task to overall fitness are unknown, so that slight changes in traits such as Swimming Efficiency may have a disproportionately large impact on fitness (42). Furthermore, natural selection operates primarily on tiny variations in fitness that are difficult or impossible to observe experimentally (43). Last, Swimming Efficiency is

a fundamental motility parameter and is likely to contribute to many other higher-level tasks, so its effect on overall fitness is probably compounded. For instance, not only is Chemotactic SNR enhanced by curvature due to its dependence on Swimming Efficiency, but overall chemotactic ability will depend on how quickly the cell can swim toward better conditions, in addition to the reliability of its gradient measurements. Experiments with marine bacteria, which tend to be fast-swimming but live in a nutrient-poor environment, have confirmed a strong relationship between swimming speed and overall chemotactic ability (44). Nonetheless, it is possible that our Pareto optimality approach, due to its insensitivity to absolute performance differences (*SI Appendix, section 12*), could lead to overinterpretation of the importance of tasks like Swimming Efficiency that seem to exhibit small variations across morphospace. Further experimental work, especially quantification of flagellar morphologies and swimming kinematics, is warranted to further inform efforts in this field.

The diversity of bacterial morphologies found in nature is reminiscent of the perhaps even larger diversity in marine phytoplankton, which prompted the “the paradox of the plankton” posed by Hutchinson (45). The paradox asked how there can be such a wide range of phytoplankton species, all competing for the same resources in the same habitat, despite the competitive exclusion principle predicting that one species should eventually outcompete the rest. Many resolutions of the paradox note that the open ocean is not a homogeneous habitat as originally thought, but quite spatially and temporally complex at small scales, so that species actually occupy different ecological niches (46). Similarly, while the diversity of bacterial morphologies coexisting in environments such as biofilms (47) or the human gut (48) might seem paradoxical, this level of habitat classification is far too coarse to be relevant to bacteria. In contrast to macroscopic organisms (49), our understanding of the niches occupied by bacteria is extremely limited. Nonetheless, our results provide testable predictions for which tasks, and perhaps microniches, different rod-shaped morphologies are specialized. For example, highly elongated species should display very effective chemotaxis and therefore might be adapted to habitats with shallow nutrient gradients. Species with high curvature, being efficient swimmers, might tend to live in oligotrophic or highly viscous environments—for instance, while seawater is of low viscosity on average, there is mounting evidence of significant spatial and temporal variation due to phytoplankton exudates and other factors (50). The low cost of construction we predict for nearly spherical bacteria is difficult to observe, but one might speculate a correlation between ease of construction and growth rate. While controlling for the many confounding factors that vary across species is challenging, we anticipate that advances in experimental (51) and phylogenetic methods (52) will enable direct tests of these predictions.

Methods

Survey of Observed Shapes. We examined all images in Bergey's *Manual of Systematic Bacteriology* (5–9) and *The Prokaryotes* (53) for curved rods. We additionally filtered an in-house manually collected dataset of bacterial morphologies compiled according to the methods of ref. 54 for all species that were reported as “curved,” “slightly curved,” “bent,” “kidney-shaped,” “crescent-shaped,” “comma-shaped,” “crooked,” “C-shaped,” or “boat-shaped.” We then searched for these species (via genus) on <http://www.bacterio.net/> and scanned the publications listed there for images of cells; if this failed, we tried a Google Scholar search for publications on the species. We restricted our searches to bacteria identified to species level, known or likely to exhibit swimming motility (i.e., flagellated, or swimming motility demonstrated for all other members of genus), and to images that contained at least some perceptibly curved individuals (see *SI Appendix, section 1*, for full details of the methodology). In all, our dataset consists of 4,903 individual bacteria across 363 images (*Dataset S2*).

Our morphology measures (elongation L and curvature K) were determined after semiautomatically segmenting the cells using the “Rod-Shaped” shape

type in MicrobeJ (23) (*SI Appendix, Fig. S1 and section 1*). Each segmented image was manually inspected to ensure accuracy of all measurements.

We computed unweighted species medians of \mathcal{L} , \mathcal{K} , and equivalent spherical diameter by first taking medians within each image, aggregating multiple images into one dataset for this purpose when they were stated to represent identical conditions (e.g., strain, substrate, nutrient conditions, etc.). We then calculated the medians of these values across all images found for each species, regardless of strain (*Dataset S3*). Using means instead of medians yielded similar results and did not affect our conclusions.

To calculate GoF between the theoretically Pareto-optimal regions and observed bacterial shapes, we computed a polygonal boundary similar to a convex hull around the latter data points (*SI Appendix, Fig. S2*; see *SI Appendix, section 1* for more details).

Model Geometry. The bacterial cell body was modeled as a curved rod of circular cross section with hemispherical caps on both ends. It has been suggested that all curved-rod bacteria are actually short sections of a 3D helix (37), but for simplicity we assume that the cell centerline always lies in a plane. All cells had a constant, arbitrary (*SI Appendix, section 6.1*) volume of $1 \mu\text{m}^3$, so each body shape was determined by two dimensionless aspect ratios: $\mathcal{L} = \ell/d$, which describes elongation, and $\mathcal{K} = \ell/(2\pi r)$, which describes the degree of centerline curvature of the curved rod shape, where ℓ is the total arclength of the body centerline (from pole to pole), d is the body diameter, and r is the radius of curvature of the body centerline (Fig. 1, *Inset*).

The flagellum was modeled as a modified right-handed helix of finite circular cross section (radius, $0.03 \mu\text{m}$) parameterized by amplitude a , wavelength λ , and number of wavelengths n_λ , as in Shum et al. (24) (*SI Appendix, section 6.2*). The flagellum axis was aligned with the cell centerline at the rear body pole for simplicity (Fig. 2 *B–D* and *SI Appendix, Fig. S3*). However, we note that there is considerable uncertainty as to the orientation in real cells; we briefly tested an alternative orientation of the flagellum (*SI Appendix, section 6.2 and Fig. S4*) but found that it resulted in inferior Swimming Efficiency for all body shapes (*SI Appendix, section 11.1 and Fig. S17*).

Numerical Solution for Swimming Kinematics and Rotational Diffusion. A regularized Stokeslet Boundary Element Method (*SI Appendix, sections 3 and*

4) was used to numerically solve for the inertialess kinematics (*SI Appendix, Fig. S5*) of freely swimming cells (*SI Appendix, sections 7 and 8*) propelled by a rotating flagellum in water, i.e., their effective swimming speed \bar{U}_{swim} and average power dissipation by the flagellar motor \bar{P}^M . This type of numerical method has been used extensively to model swimming microorganisms; our approach generally follows that of Smith (55) with several performance improvements detailed in *SI Appendix, section 5*. We also used this code to quantify the anisotropic Brownian diffusion (30) of curved-rod bacteria, accounting for the stabilizing effect of the flagellum in the case of Chemotactic SNR (56) (*SI Appendix, section 10.4*). Specifically, we calculated the timescale for loss of orientation τ , which depends on the rotational diffusion coefficients for rotations around the two principal axes normal to the swimming direction (16) (Fig. 2C and *SI Appendix, sections 10.5.1 and 10.6.1*).

Pareto Optimality and GoF. For each putative set of evolutionarily crucial tasks (out of 38 combinations), we sampled the interpolant of each task's performance landscape throughout a discretized grid of 125×100 points in morphospace, and removed the dominated points, which are beaten at all tasks by at least one other point (full details in *SI Appendix, section 12*). For each set of tasks, we computed Hargrove et al.'s (57) GoF parameter between the resulting Pareto-optimal region of morphospace and the boundary around observed species shapes as $\text{GoF} = [R_C / (R_B + R_C)] [R_C / (R_A + R_C)]$, where R_A is the area within the observations but outside the optimal region, R_B is the area within the optimal region but outside the observations, and R_C is the area shared by both the observations and optimal region (*SI Appendix, Fig. S18 and section 13*).

Code Availability. The computer code used in this work is available at <https://github.com/rschuech/RSBEM> under the GPL 3.0 license; note that it is under active development.

Data Availability Statement. The relevant data supporting the findings of this study are available as supplementary data (*Datasets S2 and S3*).

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